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The persistence of spatial interference after extended training in a bimanual drawing task

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ABSTRACT

Many studies of bimanual coordination have focused on the pervasive interference observed when people plan and produce non-symmetric movements. We investigated how the interference observed in one challenging bimanual task, simultaneously drawing non-symmetric three-sided squares (e.g., U and C), is modulated by practice. We assessed whether the benefits of practice were limited to the trained patterns or reflected the development of a more general ability for independently controlling movements of the two hands. We combined four orientations of a three-sided square, with one orientation assigned to each hand, to generate a set of 16 patterns. Participants were trained for six days with eight of the patterns. In the last two sessions, all 16 patterns were tested. The untrained patterns involved a shape that had not been practiced by one hand or a novel configuration of two practiced components. While a substantial reduction in inter-manual interference was observed over the extensive training period, participants remained much slower to plan incongruent shapes compared to congruent shapes. Incomplete generalization was observed when the new patterns were introduced. Planning time was shorter and accuracy higher for the trained patterns, but this effect was only observed in the first generalization session. There was little difference in performance between new patterns that involved an unpracticed shape or an unpracticed configuration. These results indicate that spatial interference was not eliminated with extensive practice. This persistent interference effect stands in contrast to the minimal interference observed when the gestures are conceptualized as a single action or do not involve the transformation of abstract spatial codes. The results suggest that a primary difficulty in bimanual drawing results from limitations in translating abstract goals into actions, a fundamental prerequisite for praxis.

People are quite skilled in coordinating the gestures of the hands to achieve a common goal. This coordination is evident when the hands act upon a common object; for example, when we pull the cork from a bottle of wine. It can also be seen when the two hands are used to manipulate distinct objects such as when one hand is used to manage the steering wheel while the other operates the stick shift. While such forms of bimanual coordination appear to be performed

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with little effort, most studies of bimanual coordination have emphasized that our ability to independently control our two upper limbs can be quite limited (Ivry et al., 2004). Research on bimanual rhythmic movements has emphasized strong spatiotemporal constraints that limit stable performance to certain phase relationships (Heuer, 1993; Heuer et al., 2001). These constraints are also observed in tasks involving discrete gestures. For example, people can have difficulty producing simultaneous reaching movements of different amplitudes or different directions (Kelso et al., 1979; Heuer et al., 1998) compared to conditions in which the movements are symmetric.

One task which has been used to explore the functional and neural basis of bimanual coordination requires participants to simultaneously draw two three-sided squares, one with each hand (Fig. 1). People have little difficulty on this task when the two target shapes are identical or symmetric across the vertical axis. However, when neither of these conditions are met, there is considerable cross-talk between the gestures of the two hands (Franz, 1997; Franz et al., 1996, 1991). For example, if the target shapes involve a 90° rotation, participants take a longer time to initiate the movements and can show substantial deviations in the trajectories. As in the research on rhythmic movements, these interactions can be seen as a form of strong spatiotemporal coupling.

Research with split-brain patients has provided important insight into the psychological and neural level at which this coupling arises. These patients show no measurable difference in performance between trials in which the target shapes are symmetric (i.e., congruent) compared to when they are orthogonal (i.e., incongruent). Their latency to begin the first movement or subsequent segments is similar for congruent and incongruent movements, and the quality of the trajectories is indistinguishable for the two movement classes. Interestingly, the gestures of the patients' two hands are not independent. While there is little evidence of spatial cross-talk, the initiation time for each gesture is tightly synchronized between the two hands. Thus, the absence of the corpus callosum eliminates neural interactions that underlie spatial coupling while having little effect on temporal coupling, at least for these types of gestures (see Kennerley et al., 2002).

The split-brain research allows us to draw some inferences concerning the sources of inter-manual interactions observed in studies of bimanual coordination. It is unlikely that the constraints underlying cross-talk between the two hands are due to biomechanical factors or interactions that arise at lower levels of the nervous system (e.g., interactions of spinal interneurons) given the assumption that these sources of constraint would remain operative in split-brain individuals. The dissociation of spatial and temporal coupling suggests

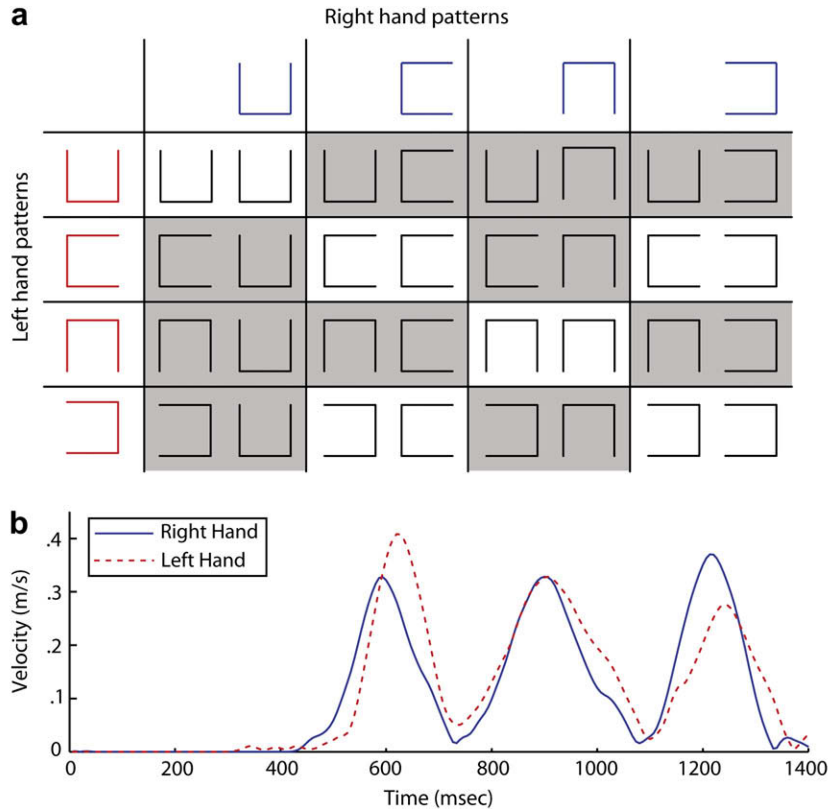

Fig. 1 – The complete stimulus set and a representative velocity profile from one trial. (a) The stimulus set was formed by the factorial combination of the four orientations of three-sided squares. Congruent patterns (no shading) were pairs involving translational or reflective symmetry; the remaining patterns were incongruent (shaded). Eight patterns were selected for training, subject to the constraints that three were congruent and one row was completely excluded. (b) The velocity profile from a trial in which the participant produced a congruent pattern. Similar to most trials, the movements of the two hands were closely synchronized for each of the three segments.

that these sources of constraint can reflect separable neural mechanisms. Temporal coupling for discrete gestures likely has a subcortical locus of origin (see Ivry and Hazeltine, 1999). In contrast, spatial interactions involve communication between the cerebral hemispheres.

Subsequent work in our laboratory has explored the level of representation at which this communication occurs (Albert et al., 2007; Diedrichsen et al., 2001, 2003). To this end we simplified the task, focusing on the contrast of single-segment movements in which each hand moves to a square positioned to the side or in front of a starting position. In this way, the bimanual movements either follow congruent (e.g., both forward) or incongruent (e.g., one forward, one sideways) trajectories. The primary independent variable is the manner in which the required movements are represented. In symbolic cueing conditions, central cues such as letters specify the required trajectory for each hand. Under these conditions, the time to initiate incongruent movements is considerably longer than the time to initiate congruent movements, consistent with the performance on the three-sided drawing task. In direct cueing conditions, the cues appear at the target locations; for example, the target outlines are filled in. Under these conditions, participants show no increase in RT on incongruent trials. In fact, the time to initiate the two movements is comparable to that observed on unimanual trials.

The fact that spatial interactions are reduced in conditions in which the actions are directly cued indicates that this source of constraint arises at relatively abstract levels of action planning. If these limitations were related to motor execution or motor programming, we should expect that performance would be similarly constrained for direct and symbolic cues given that the trajectories are essentially identical in the two conditions. Thus, the primary source of constraint appears to be related to processes associated with the translation of the symbolic cues into desired trajectories. We have argued that this translation process involves the assignment of abstract spatial goals (e.g., move forward) to particular effectors, and that the interference observed on incongruent trials arises because these representations engage a common process, rather than being independently coded for each hand. This hypothesis is consistent with recent fMRI data showing increased activation in intraparietal cortex of the left hemisphere for symbolically cued actions (Diedrichsen et al., 2006). This lateralization suggests that the translation of the symbolic cues into movements involves a common neural locus for both left and right hand movements.

Direct cues provide one way in which bimanual interference can be abolished. A different approach is to introduce manipulations that lead participants to conceptualize the two actions as components of a single action goal. For example, Swinnen et al. (1997) demonstrated that people can produce circles 90° out of phase (a bimanual action that is quite difficult to produce and maintain in most circumstances) with remarkable accuracy and stability. Of critical importance, the experimental method provided the participants with feedback that integrated, in a unitary fashion, the position of the two hands. In particular, the feedback indicated the relative phase of the two movements rather than the position of each hand independently (see also Franz et al., 2001; Mechsner et al., 2001). This work suggests that, to some degree, bimanual interference is the result of an inability to simultaneously maintain representations of two action goals when those goals are incompatible with each other (Ivry et al., 2004; Swinnen and Wenderoth, 2004).

Many studies of bimanual coordination can be viewed as a form of dual-task performance, with the gestures of each hand constituting one task. The dual-task literature has emphasized that a critical source of constraint arises from limitations in processes associated with response selection (see Pashler, 1994 for review). In the typical dual-task study, the two tasks are performed in succession and have little overlap. While perceptual processes may operate in parallel, the literature suggests that a bottleneck is typically imposed at response selection. In bimanual drawing studies, a similar constraint may arise to minimize cross-talk between the two tasks. By this logic, the absence of interference with direct cues can be attributed to the minimal demands placed on processes necessary for response selection, including the mapping of abstract symbols onto their associated responses.

The linkage of bimanual coordination and dual-task performance suggests another way in which bimanual interference might be eliminated: practice. Schumacher et al. (2001) reported that dual-task interference could be eliminated with extensive practice, at least for tasks in which the stimuli and responses for the two tasks did not overlap. After five days of practice, participants were able to simultaneously perform a pitch discrimination task (entailing vocal responses) and a visual spatial discrimination task (entailing manual responses) as quickly and accurately as when either task was performed alone. These results were interpreted as demonstrating that the constraints underlying dual-task performance are not structural in nature. Rather, dual-task limitations reflect the operation of strategic control processes that minimize cross-talk between the two tasks. With practice, the operations required for each task become highly efficient and, in this way, segregated from one another.

In the current report, we employ a similar strategy, evaluating how bimanual interference is affected by extended practice. We used the drawing task introduced by Franz et al. (1996) in which the participant simultaneously is required to draw two three-sided squares, one with each hand. Over two weeks, participants practiced drawing 8 of the 16 possible patterns (training set), followed by two days of testing on the full set of 16 patterns.

We assumed that practice would lead to improved performance. Of critical interest was whether this improvement would lead to the elimination of all bimanual interference – that is, would participants be equally adept in producing congruent and incongruent movements? By requiring the movements to be initiated simultaneously, we are, in effect, adopting the dual-task procedure of Schumacher et al. in that there is no priority given to one task (movement) and there is no experimenter-imposed delay between the two tasks (e.g., stimulus-onset asynchrony). We recognize, however, that, unlike Schumacher et al. (2001), the two tasks do not involve non-overlapping stimuli and responses; indeed, the overlap is considerable. Nonetheless, it is possible that with extensive practice, participants might learn to segregate the two movements or come to conceptualize the stimuli as defining a common goal. The inclusion of the generalization phase should provide insight into the changes that occur with learning (see Hazeltine et al., 2002). In particular, if the benefits of learning are restricted to the practiced combinations, then we can assume that the participants have learned to produce specific gestures. In contrast, if we observe generalization, then the benefits of training must be operating at a more abstract level of representation.

1. Methods

1.1. *Participants*

Six individuals were recruited for the experiment. Each participant was tested on a daily basis over a two-week period and received financial compensation. One participant was excluded from the analyses for failing to comply with the instructions; this participant indicated that he did not always produce speeded responses, but rather sought to maximize accuracy. Thus, the final sample included five right-handed individuals (two men, three women). The protocol, which complied with the Declaration of Helsinki, was approved by the institutional review board of UC, Berkeley and all participants provided informed consent.

1.2. *Apparatus and stimuli*

A two-dimensional virtual environment was used for stimulus presentation and online visual feedback (see Diedrichsen et al., 2001, Fig. 1). The environment was composed of a table (110 × 77 × 75 cm), a projection screen positioned 48 cm above the table surface, and a reflecting mirror mounted halfway between the table and screen. Stimuli were presented from a DLP projector, mounted on the ceiling above the screen. By viewing the stimuli through the mirror, the participant had the illusion that the stimuli were presented directly on the table surface.

The target shape for each hand was a three-sided square, with the open side facing up, right, down, or left. When presented on the screen, each side spanned 10 cm. Combining these four patterns for the left and right hand created a stimulus set of 16 patterns (see Fig. 1). Six of these pairs were termed congruent due to translational or reflective symmetry about the vertical axis; the other 10 patterns were termed incongruent. Eight of the patterns were selected to create the training set (three congruent and five incongruent), with the exact pairs varied between participants. The training sets were created such that one of the four shapes was never produced by the left hand. The other eight patterns constituted the generalization set (three congruent and five incongruent). Four included a shape that had never been drawn by the left hand during training (novel shapes), and four included two shapes that had been well practiced, but had never been produced together (novel configurations).

All movements were produced on the table surface. A magnetic three dimensional movement tracking system (mini-BIRD, Ascension Technologies) was used to record the position of the participant's hands. Two small transmitters (15 × 7 × 7 mm) were taped to the tip of the left and right index fingers. Although the mirror occluded vision of the hands, feedback was provided in the form of small white dots (2 mm diameter) that appeared on the table surface. The position of the sensors at each sample remained on the screen throughout the trial. Given the sampling rate of 140 Hz, feedback allowed the participant to virtually draw on the table surface.

1.3. *Procedure*

The start of each trial was denoted by the appearance of two starting circles (5 mm diameter), located 35 cm in front of the participant and separated by 40 cm. The participant moved their hands into the starting circles and was required to maintain this position for 1 sec. Then, a "+" sign appeared between the starting circles on the vertical meridian. This served as a fixation point. After maintaining the starting position for an additional variable delay of 1–2 sec, the target pattern appeared as two white, three-sided squares. One shape was presented to the left of fixation and the other to the right of fixation, 40 cm in front of the starting circles. The cues indicated the target shape for each hand and served as the imperative signal.

The participant was instructed to reproduce the target shapes "simultaneously" and as quickly and as accurately as possible. We did not specify which endpoint of the three-sided square was to serve as the starting point. The participant was required to produce the shapes by moving their index fingers along the surface of the table surface. They were to lift their fingers off the table when the drawings were completed. A bonus score, based on the time from the presentation of the stimulus until the end of the drawings, was provided after each trial to motivate the participant to move as quickly as possible. The bonus was only provided if the drawings met a set of accuracy-based criteria (e.g., did not have more than three sides and overall orientation matched the target shapes). The experimenter monitored performance and indicated via a keyboard, whether a trial had been scored as accurate (and subject to bonus points) or erroneous.

The experiment was divided into two phases, training and generalization, although the participant was not informed of the transition between the two phases. The training phase consisted of the first six days. On day 1, there was a 32-trial practice block in which the eight patterns were presented four times each. Following this, and on all subsequent days, the participant completed 12 test blocks of 32 trials each. Thus, each pair was tested 48 times on each day of training, for a total of 288 reproductions per pattern. Generalization was assessed on days 7 and 8. Here all 16 patterns were tested, twice per pattern per block.

The bonus criterion was adjusted on an individual basis. The mean time to complete the drawings (including the RT interval) on the practice block of day 1 established the initial criterion. For the test blocks, money was earned whenever the pattern was accurately completed within 500 msec of their criterion time. One cent was earned for each 100 msec below the criterion on a trial-by-trial basis. The mean time on the sixth block on each day was used as the bonus criterion for the next day. Overall, participants earned between $6 and $12 per session above a base reimbursement rate.

1.4. Data analysis

An algorithm was used to segment the kinematic traces. We calculated changes over the x and y axes, using the greater value to define the principal heading. The principal heading of each hand was identified for each sampled finger position after smoothing over three consecutive samples. Changes in heading were marked as points in which a new principal heading was observed for three consecutive samples. Trials in which there were only three principal heading transitions (including the initial heading), each of which matched the relevant target shapes, were scored as correct.

For these trials, a set of temporal and spatial dependent variables was calculated. Reaction time was defined as the interval between the onset of the stimulus and time at which hand velocity exceeded 5% of the maximum velocity for the first line segment. A similar velocity criterion was used to define the onset of the second and third segments. The end of each segment was marked as the point in which velocity fell below 5% of the maximum velocity for that segment. Note that while this criterion over-estimates the inter-segment pauses, the participants almost always produced straight, rather than curved segments. The onset and offset times for each segment allowed us to calculate the inter-segment pauses prior to the initiation of the second and third segments, as well as the total planning time, defined as the sum of the reaction time and two inter-segment pauses.[1] The time between the onset and offset of each of the three segments were summed to quantify movement time. Temporal asynchrony was defined as the difference between the onset times for each of the three segments.

Intra-hand spatial measures included the length of each segment and the angle between successive segments. Inter-hand spatial measures were based on the absolute difference between the left and right hands for these measures.

2. Results

2.1. Training phase (days 1–6)

2.1.1. Temporal measures

Over the six days of training, participants became much more adept at the task. The mean planning time (RT plus inter-segment pauses) of each participant decreased, as did the movement time. Statistical analyses were performed with a 6 (day) × 2 (congruence) ANOVA. A main effect of day was observed for planning time, $F(5,15) = 6.89$, $p = .002$, and movement time, $F(5,15) = 2.90$, $p = .05$. As expected, the effect of congruence was highly significant for planning time, though the effect on movement time also reached significance.

A primary question under investigation here is whether spatial interference is eliminated with extensive practice. The day × congruence interaction was reliable for planning time, $F(5,15) = 8.939$, $p < .001$ reflecting the fact that the degree of improvement over sessions was greater for the incongruent trials compared to the congruent trials (Figs. 2 and 3). Nonetheless, even at the end of the sixth practice session, there is a substantial cost (339 msec) for incongruent trials, relative to congruent trials. Performance had not reached asymptotic level by session 6; as such, it is possible that this persistent cost might be eliminated with even more extensive practice. No interaction was present for movement time, $F(5,15) = 1.002$, $p = .437$. The mean movement time was reduced by 363 msec on congruent trials (953 msec on day 1; 590 msec on day 6) and 444 msec on incongruent trials (1140 msec on day 1; 696 msec on day 6).

The participants generally paused between successive line segments. This suggests that the participants may have only partially planned segments 2 and 3 prior to the onset of the first line segment, using these pauses to complete planning for the next segment. Pauses were longer for incongruent pairs than congruent pairs prior to the third segment [turn 2: $F(1,4) = 14.19$, $p = .03$] but not prior to the second segment [turn 1: $F(1,4) = 2.65$, $p = .20$]. Interestingly, when just considering pause durations, the congruence effect did not decrease with training (day × congruence interaction, $F < 1$ for both pause durations).

The drawing motions of the two hands were tightly synchronized for each segment. While we expect this reflects a fundamental constraint on performance, it was also part of the task instructions in this study. On average, the dominant, right hand began moving slightly earlier than the left hand (15 msec, 7 msec and 19 msec for each of the three segments, respectively), although these values were not significantly different than zero. The asynchrony measures did not vary across sessions ($F < 1$), congruence, ($F < 1$), nor was the interaction reliable ($F < 1$).

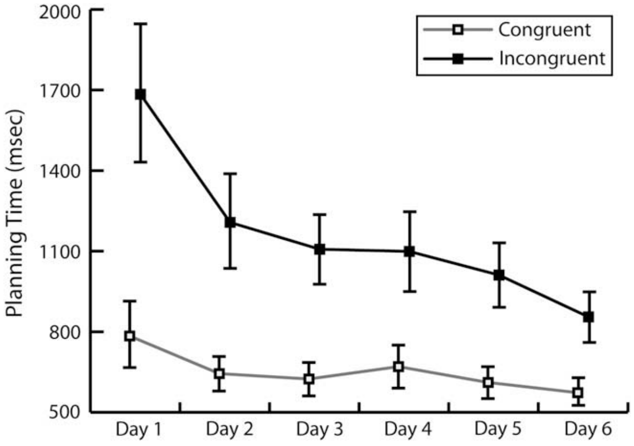

Fig. 2 – Planning times during the training phase. Planning time is defined as the sum of reaction time and the pauses that occurred prior to the start of the second and third segments. Participants became faster with practice, although there remained a substantial difference between incongruent patterns (black) compared to congruent patterns (grey). Error bars indicate +/− the standard error of the mean.

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[1] We recognize that planning for the second and third segments could also occur during the movement phases. The overall pattern of the results does not change if the analysis is based on the total time needed to complete the drawings (reaction time plus pauses plus movement time) or the reaction time alone.

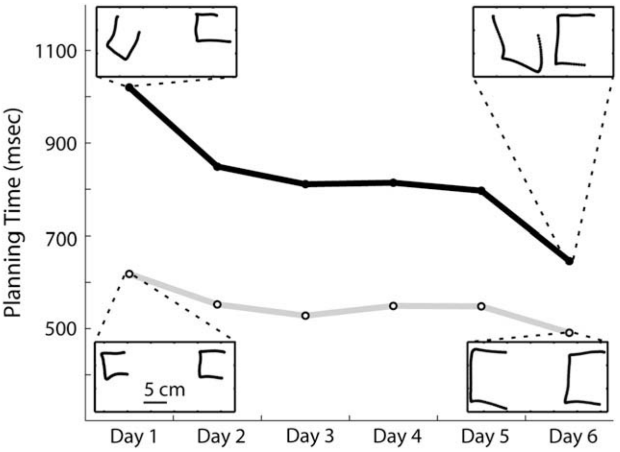

Fig. 3 – Planning times for an individual participant during the training phase. This participant showed the smallest congruence effect of all of the participants at the end of training. Nonetheless, there remained a substantial difference between the planning time for incongruent patterns (black) compared to congruent patterns (grey). Example trials are shown for each class of patterns at the beginning and end of training. The scale for all of the movements is indicated in the lower left example. Consistent with that observed in the group data, this participant showed a substantial reduction in planning time with little change in accuracy for the incongruent patterns.

2.1.2. *Spatial measures*

In terms of overall accuracy, the reproductions were judged to match the target pattern on 97% of the trials in the congruent condition and 92% of the time in the incongruent condition, $F(1,4) = 14.00$, $p = .02$. No changes were observed across sessions for this qualitative measure of accuracy, $F(5,20) = 2.02$, $p = .12$.

As noted above, our more detailed analysis of the trajectories is restricted to trials scored as correct. Segment length was highly correlated across trials (congruent: $r = .95$; incongruent: $r = .87$). However, these high correlations are driven by the considerably variability in segment length across trials. At a more microscopic level of analysis, we compared the difference in segment length for the right and left hands. This difference (absolute value) was greater on incongruent trials compared to congruent trials for each of the three segments [segment 1: $F(1,4) = 8.50$, $p = .043$; segment 2: $F(1,4) = 22.95$, $p = .009$; segment 3: $F(1,4) = 7.90$, $p = .048$]. The segment lengths became more similar with practice for the second segment, $F(5,20) = 3.15$, $p = .03$. A mean segment length difference of 7.6 mm on session 1 was reduced to 1.5 mm on session 6. Although this trend was present for the other two segments, the interaction was not reliable for segment 1 or segment 3.

Perfect performance would lead to 90° changes in principal heading at each transition. Radical departures from this value would lead a trial to be classified as incorrect. As only correct trials are included, this biases our results to underestimate differences between congruent and incongruent trials given that error rates were higher in the latter condition. As with the segment length data, we analyzed the absolute difference between the angles produced by the two hands on a segment by segment basis. The difference was greater for incongruent trials (mean = 11.68°, SEM = 1.42°) than congruent trials (mean = 7.99°, SEM = .47), $F(1,4) = 7.85$, $p = .049$. Interestingly, there was no significant improvement over the six days of training [$F(5,20) < 1$], and no differential improvement for the incongruent and congruent trials [$F(5,20) < 1$]. The results here were similar for both heading transitions.

In summary, participants were able to reduce their planning time and move more quickly after extended practice. These improvements were greater for incongruent pairs than congruent pairs. However, in terms of spatial measures, there was little change in the quality of the drawings with practice. Spatial distortions of the cued patterns remained consistent for the incongruent trials over the six days of training.

2.2. *Test phase (days 7 and 8)*

During the test phase, participants were tested with the full set of 16 stimuli, eight of which had never been practiced during the training phase. Analyses were limited to measures that either improved during training or varied with the congruence of the shapes drawn. The data were analyzed with a three-factor ANOVA of session (day 7 or day 8) × congruence × pattern (practiced *vs* new). Planned contrasts were used to compare the two types of new patterns (novel shapes and novel configurations).

2.2.1. *Temporal measures*

In terms of planning time, the main effect of congruence was highly reliable during the generalization phase. Participants remained slower in initiating and planning their movements when the two shapes were incongruent compared to when they were congruent, $F(1,2) = 83.92$, $p = .012$. Significant improvements occurred by the second day of testing [main effect of session: $F(1,2) = 166.886$, $p = .006$].

Most interesting, the main effect of pattern was reliable [$F(2,4) = 7.451$, $p = .045$]. As can be seen in Fig. 4, planning times were longer for the new patterns, especially those that were incongruent (205 msec longer) relative to trained patterns. This effect was reduced to just 67 msec by the second day of the test phase. We assume that there was considerable generalization given that planning times on the new patterns on day 7 were much faster than planning times for the training set on day 1 (compare Figs. 2 and 4). Our design does not allow a within-subject assessment of this hypothesis because we did not obtain a baseline measure of performance on the new patterns at the beginning of the training session. However, because the novel shape and configurations were counter-balanced across individuals, it is very likely that the planning times for the new patterns indicate some degree of generalization. There was also a considerable increase in the planning times from day 6 to day 7 for the trained patterns. This effect persists in both the congruent (126 msec) and incongruent (389 msec) configurations, and is likely a carry-over effect due to participants becoming more cautious as they experienced difficulty due to the introduction of untrained configurations. This provides further evidence

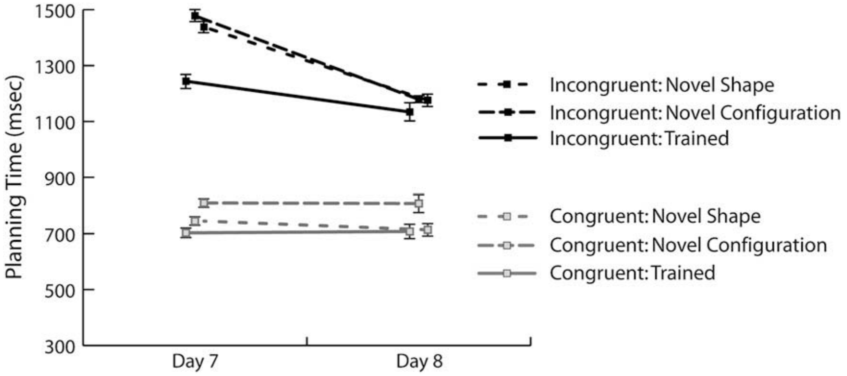

Fig. 4 – Planning times during the generalization phase (days 7 and 8). An increase in planning time was found for the new patterns, especially on incongruent trials. This increase was similar for the novel shape and novel configurations. By the second day of practice, the costs associated with the new patterns are almost entirely eliminated. Error bars indicate +/− the standard error of the mean.

that participants did not distinguish between the new and trained configurations.

To evaluate the specificity of the slowing on the untrained configurations, we compared the two types of new patterns. Based on an ANOVA of just these patterns, we observed a main effect of congruence [$F(1,3) = 34.98$, $p = .01$], session [$F(1,3) = 91.04$, $p = .002$], and a marginally reliable interaction of these factors, $F(1,3) = 6.87$, $p = .08$. The effect of pattern was not reliable, $F(1,3) = 5.76$, $p = .1$, nor did this factor interact with either of the other factors (each $F < 1$). Planned comparisons were used to contrast the two types of new patterns to the trained patterns. For incongruent trials, an increase in planning time on session 7 was reliable for both the novel shapes [mean increase = 234 msec, $t(4) = 4.25$, $p = .013$] and the novel configurations [mean increase = 194 msec, $t(4) = 3.03$, $p < .039$], relative to trained patterns (mean = 1244 msec). For congruent trials, the small increase was also reliable for the novel shapes [mean increase = 107 msec, $t(4) = 3.06$, $p = .038$], but failed to reach significance for the novel configurations [mean increase = 65 msec, $t(4) = 1.80$, $p = .146$], relative to the trained patterns (mean = 699 msec). In sum, participants were slower to plan the new patterns compared to the trained patterns, and this cost was not influenced by whether the new pattern required the production of a shape that had never been practiced or the production of a novel configuration of two well-practiced shapes.

The increase in planning time for the new patterns was only observed in the initial reaction time. There was no difference between the trained, novel shape, and novel configuration patterns in terms of the duration of the pauses prior to segments 2 and 3 [$F(2,4) < 1$ and $F(2,4) = 1.28$, $p = .37$, respectively].

As with performance during training, the gestures of the two hands were tightly synchronized. Overall, movement of the right hand preceded the left (20 msec, 2 msec and 21 msec for each of the three segments, respectively). These asynchrony values were similar for the new and trained patterns.

2.2.2. *Spatial measures*

The accuracy data mirrored that observed in the temporal measures. There was no reduction in accuracy for the new patterns on congruent trials, although our ability to detect differences here is hampered by the fact that accuracy is near ceiling. On incongruent trials, performance on the new patterns (93%) is lower than for the trained patterns (97%), $t(4) = 5.66$, $p = .004$. Unlike the measure of planning time, the accuracy difference between trained and probe trials persisted during the second test session. No differences in terms of accuracy were observed in a direct comparison of the novel shapes and novel configurations conditions, $t(4) = 1.041$, $p = .36$.

2.2.3. *Awareness*

Only one participant spontaneously reported that they were aware on the introduction of new patterns on day 7, and this report was limited to the new shapes. None of the participants reported being aware of the novel configurations, either in terms of their spontaneous reports or in an informal survey following day 8. Nonetheless, all of the participants reported in the survey that their performance "deteriorated" on day 7, and in most cases attributed it to intrinsic sources (e.g., "I couldn't get my hands to work properly today."). The feedback also helped make salient that performance was adversely affected on day 7 since the participants were not able to meet the bonus criteria on this day.

3. Discussion

The present study examined the effect of extended practice on a bimanual task in which each hand was required to draw a distinct shape. As would be expected, people became much more proficient with practice. This benefit, at least in absolute terms, was most pronounced in those conditions that were initially most challenging: when the shapes (and movements) were asymmetric. Nonetheless, even after over 2000 trials of practice, a substantial cost remained on the incongruent trials. The benefits of practice were not limited to the specific patterns used during training. There was considerable savings in performance when a set of new patterns was introduced during the last two sessions, although this transfer was not complete. Interestingly, the savings appear to reflect the development of abstract skills related to this bimanual drawing task. Generalization was similar for patterns involving a novel shape or novel configuration of well-practiced shapes.

The generalization phase provided a probe on the representational changes that occurred with practice. Studies of transfer in sequence learning tasks indicate that training leads to the establishment of effector-independent representations. For example, Grafton et al. (1998) observed near-perfect transfer between two effector systems. During training participants produced sequences with the fingers of their right hand, eliciting learning related changes in the contralateral sensorimotor cortex, ipsilateral supplementary motor cortex, the inferior parietal lobe, and the contralateral anterior cingulate. During transfer, the responses were produced with arm movements. Activation remained high in both the inferior parietal region and the anterior cingulate, suggesting these areas are involved in the representation and activation/maintenance of effector-independent (i.e., abstract) action representations. However, the limited number of studies involving extensive, multi-session practice suggest that, over time, the learned representations are effector-specific; for example, minimal inter-manual transfer is observed following multi-week training on a finger movement sequence (Karni et al., 1995).

The current study looks at a different aspect of skill acquisition, the ability to coordinate the gestures of the two hands when the goals of these actions are not explicitly integrated. The generalization results favor the hypothesis that learning did not involve mastering the specific shapes produced by each hand. There were essentially no differences in performance between patterns that involved a novel shape from those that involved novel configurations. Thus, the benefits of practice here likely involve more generic aspects of this demanding configuration task.

Past experiments have shown that the constraints underlying bimanual interference are not related to motor execution or programming, but rather reflect limitations that arise at more abstract levels of planning. Mechsner et al. (2001) showed that patterns of bimanual stability could be radically altered as a function of the perceptual consequences of the actions. Swinnen et al. (1997) demonstrated that very difficult bimanual patterns can be produced accurately when the feedback provides an integrated representation of the desired pattern.

These effects are not limited to perception, or fully accounted for by perceptual models (Albert et al., 2007). In contrast to the pronounced bimanual interference effects observed when the target locations are symbolically cued, these costs are almost entirely abolished when the target locations are indicated directly by the stimuli (Diedrichsen et al., 2001) regardless of the perceptual features of the targets (Albert et al., 2007). This dissociation has led to the hypothesis that bimanual coordination is highly constrained when either the actions for the two hands entail distinct goals or the achievement of these goals requires a translation from an abstract goal into a specific movement plan. We have previously referred to these limitations as an assignment problem. By this view, the gestures of the two hands can be produced remarkable upper limb independence when the desired action is represented as a common goal (e.g., removing the lid from a jar). Independence is also possible when the actions entail distinct goals, as long as the translation problem is minimized (e.g., reaching to directly defined targets that require neither the translation between perceptual and motor space nor the mapping of symbolic stimuli to their associated responses).

The conditions in the current experiment did not appear to meet either criterion. The patterns were always presented as two shapes and the movements involved a translation on the drawing surface. The limitations imposed by these conditions persisted after extensive practice. People certainly became more proficient at the task, but there remained substantial costs on incongruent trials relative to congruent trials.

The persistence of bimanual interference after extended training suggests that the actions of the two hands might engage a common, effector-independent mechanism with limited resources. Unimanual skilled actions, produced by either hand, have been shown to engage the inferior parietal lobe of the left hemisphere (Johnson-Frey et al., 2005). Left hemisphere lesions can lead to difficulty performing well-learned actions with either the contralateral or ipsilateral hand, as well as in coordinating the actions of both hands (Goldenberg, 2003; Geschwind and Kaplan, 1962). The asymmetric involvement of the left hemisphere in praxis is especially pronounced when the actions are symbolic in nature; for example, when they involve pantomiming intransitive gestures or involve the use of tools. We suggest that the bimanual drawing task used in the present study relies on the engagement of similar neural processes. That is, the interpretation of the two target shapes and translation into movement for both hands will engage a common left hemisphere process (Diedrichsen et al., 2006). While the operation of this process became more efficient with extended practice, the participants were not able to achieve independent control of the two hands. We assume these persistent costs reflect the demands imposed on a common left hemisphere mechanism associated with praxis for both the left and right hand movements.

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